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STENOTHERMY AND ZONE-INVASION[1]

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The conception of geographical distribution seems to have come to the botanists of the later fifteenth and earlier portions of the sixteenth centuries as a distinct and gradually developing idea. They began to realize that the plants of central and northern Europe were different from those of Greece and Italy as treated of by Theophrastus and his successors and were worthy of study for their own sakes. With the revival of learning, the discovery of the "New World" and the attention paid to the plants and animals of the different countries being made known through the visits of the various voyagers, both the knowledge of the different countries and that of the natural objects brought back from them emphasized more and more the idea of geographical differences in flora and fauna and the gradual perception that there might be some general laws or principles governing them. It remained for Humboldt in a series of papers in 1805, 1807, 1816, 1817 and 1820, to place the matter of the geographical distribution of plants on a firm scientific basis. After Humboldt's preliminary work, came the studies of a number of leading botanists and gradually there have arisen various points of view, especially as to factors concerned and as to the division of the subject into various categories according to the special factor, or set of factors, emphasized. The studies in ecology, which have come more recently to represent the activities

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toward solutions of the problems of distribution, are founded more particularly on the influence and control of distribution by edaphic factors, or those more particularly connected with the substratum and concerned in the studies of association and formations, in other words having to do particularly with topographic distribution as contrasted with climatic distribution.

Humboldt's publications concerned themselves particularly with climatic distribution, although, incidentally, he necessarily touched upon topographical distribution. The chief factor of control in climatic distribution recognized by Humboldt and his successors is temperature, and Humboldt called attention, in most graphic ways, to the resemblances between the climatic zones of latitude over the earth's surface and those of altitude passed through in the ascent from sea-level to thousands of meters above it. Those of us who are older remember the reproductions of Humboldt's diagrams of the various zones (or perhaps better, belts) of vegetation of mountain peaks situate in different latitudinal zones which were reproduced in the various atlases and older geographies. Lamouroux, in 1825 and 1826, applied the general principles of Humboldt, DeCandolle and Robert Brown, to marine plants, especially to the algæ, and distinguished latitudinal zones and differences of distribution in depth (belts), as well as the effect of certain factors on topographical distribution. Lamouroux was followed by Greville and Harvey in the attempts to discuss the distribution of marine algæ and the latter (1852) divided the Atlantic coast of North America into 4 divisions and emphasized the position of Cape Cod as a demarcation point. These authors and their ideas may be taken as starting points of the discussions more or less contemporaneous and later.

A definite attempt to determine the criteria of a climatic zone was made by C. Hart Merriam (1894, 1898) in his papers on "life-zones" and "crop-zones" of the United States. Merriam used summation indices compiled for a large number of stations and divided the

country into life-zones in accordance with the indices thus obtained. Merriam also shows that, by plotting the isotherms of 18°, 22°, and 26° C., for the six hottest weeks of the year, divisions are separated from one another corresponding in all essential details to those obtained by plotting summation lines. This is practically the method I have used in separating climatic zones of the surface waters of the oceans. Livingston and Livingston (1913) have discussed the system of Merriam and proposed a system of efficiency temperature coefficients which are claimed to represent something more of the basic principles of physiology upon which the final explanations of distribution should be based. A comparison between isoclimatic lines plotted for the United States on the direct summation basis and isoclimatic lines plotted on the efficiency indices basis shows a strong, but not absolute tendency toward agreement. The Livingstons, however, do not discuss the interpretation of their charts as regards plant distribution in detail.

Nearly 30 years ago, while attempting to obtain some idea of the temperature relations of the geographical distribution of the Laminariaceæ, I noticed a seemingly definite relation to the lines of mean maxima (summer lines or isotheres) of surface temperatures. Some brief remarks on these relations were published in 1893. Farther studies seemed to emphasize the relation between the 10, 15, 20, and 25 degree (Centigrade) isotheres or lines of mean monthly maxima and the limits of distribution of various floral groups, and in 1914 I read a paper at the Twenty-fifth Anniversary Celebration of the Missouri Botanical Garden (published 1915) as a preliminary communication on the temperature relation of the distribution of the marine algæ as expressed in terms of mean monthly maxima and minima (isotheres and isocrymes). In this paper, I made a tentative division of the surface waters of the oceans, etc., into zones according to the courses of the 10°, 15°, 20°, and 25° C. isotheres, and announced that a rough tabulation indicated that the great majority of species are confined to one or

another of these zones, that a considerable number of species extend over two of these zones, that a comparatively small number are found to extend over three zones, while the number credited with extending over four or five zones are extremely few and almost always doubtfully so accredited. It was also suggested that the disturbance of zonal distribution, so far as the occurrence is concerned, is probably due to spot distribution, *i.e.*, where waters of a higher or lower temperature than that of the zone in which they are placed exist due to local physical conditions, and to seasonal lowering of the temperature normal to the zone. In 1916, in another address (published 1917), I reasserted these statements and added something as to the significance of the isocrymal lines, or lines of monthly mean minima. I suggest using the latter lines to divide the zones into proper provinces.

Since writing the last paper I have investigated the floras of the coast of New England and have found that the species may be readily arranged in two categories, one of the colder waters (20° C. or less) and the other of the warmer waters (20° C. or over), and while some of these are found only north of Cape Cod and others only south of Cape Cod, the majority are found on both sides of the cape, which is, however, the natural dividing point and approximating closely to the position of the 20° C. isothere. The separation is made by ascertaining whether a given species of the last group in particular inhabits warmer localities to the north or is found only in cold localities or appears or fruits only in the colder season to the south. Similar examinations of other, but less perfectly known floras, add to the conviction that species of marine algæ, at least, are normal to only one zone of 5° C. amplitude as to mean maxima, except in the cases of those of the very coldest waters and it may be that they are no exceptions to such a rule. Furthermore, it may be assumed, from observing the isotheres and isocrymes in favorable portions of the surface waters of the oceans, viz., those undisturbed by the larger ocean

currents, that the normal, or at least the minimum seasonal variation in temperature is closely approximating to 5° C. This, added to the amplitude of 5° C. mean maximum variation, makes the normal amplitude of temperature within each zone about 10° C. and the temperature interval favorable to the persistence of a species within a given area, so far as active growth is concerned, is very little, if any, over 10° C. The seasonal range in some portions of the surface waters of the oceans may amount to as much as 18° or 20° C. In such localities as may have such an extreme range of temperature, we may, I think, assume that a condition of quiescence, or rigor, may exist, at least in the perennial species, such as exists in the case of perennial plants in zones on land where there is an alternation of a frost with a frostless season, as it does particularly in the polar and most of the so-called temperate regions.

It will appear from a careful consideration of what I have been saying, that the temperatures for normal persistence of any particular species of marine plant lie within narrow limits, although many marine plants are credited with extending over fairly wide ranges of temperature. We are, consequently, brought directly to a consideration of the ideas implied in the use of the terms stenothermal and eurythermal. The proposal of these terms, or rather their equivalents in German, rests with Karl Moebius who, in 1877, published a paper in *Die Natur* on the external factors of life of marine animals. According to Moebius the eurythermal animals can endure wide ranges of temperature and continue their occupation of extensive zones and range in depth because they are able to reproduce under such conditions. It is this conception of being able to reproduce at widely separated temperature limits that I wish to call particular attention in order that I may discuss it later. Moebius states that the eurythermal animals are much less numerous than those which normally occur and withstand a narrow range of temperature which he calls stenothermal animals. The latter seem to be the more

usual type and this agrees with what I have found in my attempts to tabulate the marine algæ as I have already mentioned with emphasis. To repeat the idea of Moebius, in a rather free translation of his own words, eurythermal animals are those which in the surface waters of the temperate zones are able to exist and to continue their kind through reproduction under all of the various temperature relationships of the different seasons of the year.

The terms eurythermal and stenothermal have not come into any noticeable use in botany and are not widespread even in zoological literature, although they are very convenient. They are both to be found in the later editions of Webster's and in the supplement to the Century Dictionary. They are discussed in the latest edition of the Encyclopedia Britannica by G. H. Fowler, under the article on "Plankton." Fowler says: "In relation to temperature the wide-ranging species are termed eurythermal, the limited stenothermal (Moebius); the terms are useful to record fact, but not explanatory. It seems to be the case that to every organism is assigned a minimum temperature below which it dies, a maximum temperature above which it dies and an optimum temperature at which it thrives best; but these have to be studied separately for every species." The definitions of Moebius and the comments of Fowler are exactly to the purpose of our consideration, since the one is from the purely distributional point of view expressing a fact only, while the other seeks to link the fact with some explanation, preferably physiological. Our own discussion of these terms and the underlying conceptions must necessarily proceed on a somewhat middle course, largely from the distributional point of view, but with such regard for the interpretation of the physiological basis as may be possible from our present knowledge.

It will be of the greatest assistance, I think, to consider some concrete cases of eurythermal species and to inquire into the conditions of their continued persistence

under different temperatures. One constituent of the marine flora of the northern hemisphere which has interested me very much indeed, is the common eel-grass, *Zostera marina,* a marine spermatophyte. As commonly regarded as to specific limits, this plant extends from the northern coasts of Europe down along the western coast and enters the Mediterranean Sea, occurring spotwise in the northwestern portion of it and being represented also in the northern Adriatic. *Zostera marina* is represented in one or two localities in southwestern Greenland and, reappearing at the Strait of Belleisle, it seems fairly continuous in its distribution thence down to the coast of North Carolina, at least, and is reported from West Florida and the Bermuda Islands, although I can not make certain as to whether it actually grows in either of the last mentioned stations. *Zostera marina* is reported from both the North American and the Asiatic coasts of the North Pacific, but the exact limits of its occupancy of these shores is in doubt. The greatest range of temperature experienced by the *Zostera* is that on the Atlantic coast of North America, where it extends from waters of a mean maximum of 0° C. to those of a mean maximum of somewhat over 25° C. It is also found in localities where the seasonal temperature range of the surface waters is from somewhat below 0° C. to 15° C. It ranges through all the temperature zones of surface waters from the Upper Boreal (0°–10° C.) to the Tropical (25°–30° C.), *i.e.,* five zones in all. I shall discuss the reasons for this wide extension of the range of *Zostera marina* later, but desire to call attention here to the facts that we are dealing with a perennial plant with unusually effective methods of vegetative multiplication and devices for wide dispersal.

Another eurythermal marine species is *Ascophyllum nodosum,* one of the bladder-bearing Fucaceæ or Rockweeds. On the Atlantic coast of North America, this species is found in some abundance from well up on the west coast of Greenland down to the northeastern coast of New Jersey, or on coasts having a range of mean

maximum temperature from 0° C. or below to about 22° C. and seasonal ranges of about 17° C. maximum. *Ascophyllum nodosum* is also a perennial species. *Rhodochorton Rothii* is a delicate red alga which, nevertheless, seems to be a perennial and *Monostroma Grevillei* a membranous green alga, and *Polysiphonia urceolata,* a filamentous red alga, are annuals, but with the same range as *Ascophyllum nodosum. Grinnellia americana* is the last example of many eurythermal algæ of the Atlantic coast of North America I desire to bring forward. It is a strikingly beautiful annual membranous red alga and extends from northern New England (North Temperate Zone, 15°–20° C., mean max.) to the coast of North Carolina (Tropical Zone, 25°–30° C., mean max.). Other examples of eurythermal species might be given, but those I have mentioned are typical and reasonably well known. They will serve as a good representative basis for discussion with the idea in mind that what is indicated by the eurythermy of one and another of them will, by analogy, also seem extremely possible to be the case with all other types and individual species extending over ranges of temperature of more than 10° C.

Stenothermal species are particularly characteristic of the Tropical Zone, in very few portions of which the seasonal variation in temperature is over 10° C. Species confined to the Upper Boreal or to the Upper Austral Zones are also narrowly stenothermal, since the entire range of temperature in these zones is not over 10° C. The temperate and subtropical zones are usually sufficiently affected by seasonal changes to show a range of temperature greater than 10° C., but in the southern hemisphere in particular, there are portions of these zones, at least, that show only a 10° C. range and consequently may possess stenothermal species. The annual species of any particular zone, and even perhaps all annual species, are stenothermal so far as their actively vital processes are concerned, but may endure temperatures of more extended range in the resting seed or spore condition. This naturally brings us to inquire as to the

nature of the fundamental differences between the eurythermal and the stenothermal species, and this, in turn, is closely connected, as I shall hope to make plain, with the second topic of this paper, viz., zone-invasion.

I have already tried to make clear the fact that my investigations have tended very strongly to convince me that each and every species of marine plant is normal to only one zone, and that, when a species is credited to, or found to occur in, two zones, it is normal to only one of them and is to be found in the other because for some reason it finds in the second zone the temperature conditions, both as to degree of temperature and as to duration of that degree of temperature, of the zone to which it is normal. In a similar fashion, if a species is found to inhabit three, four, or even five zones of different temperature relations, it is possible to make certain that it is normal to only one of these and invades the other zones because it finds the proper temperature conditions for its continuous existence. The proper temperature seems certainly to be that which is most intimately connected with reproduction, since it is this function that is most necessary to persistence in the particular locality. In the laboratory, under controlled conditions, algæ, in particular, have been found to be very sensitive to even slight changes of temperature, as Ewart (1896) has demonstrated. It does not seem as if the same algæ, in their ordinary environment, could be thus sensitive as West and West (1898) have held, but Ewart (1898) has answered their objections, claiming that, in nature, they are probably equally sensitive, but withstand seemingly great changes for reasons that prevent these changes actuating. This is something of the truth in the case of species invading colder from warmer, or warmer from colder zones in that they find in the invaded zones the temperatures, both as to intensity and duration, which are favorable to their growth and reproduction and which are the same as they find normally in their proper zone.

Zone-invasions proceed in one of two directions, or,

occasionally, in both. They may proceed from warmer to colder zones, they may proceed from colder to warmer zones, or they may proceed from a zone of intermediate temperatures to both colder and warmer zones. Where warmer spots or areas exist in the midst of cooler waters, species of warmer zones may exist spotwise in the cooler zone. Where certain portions of the waters of a warmer zone are depressed in temperature by cold currents or upwellings, or, for certain seasons of the year, suffer a general lowering of the temperature, there and then may species from cooler zones be expected to put in an appearance. The extent of such invasions will depend naturally upon the intensity and duration of the unusual temperature. A consideration of the examples I mentioned as typically eurythermal may serve to make this idea more clear.

Zostera marina seems, on careful study of its occurrence and habits on all the coasts where it is found, to be normal to the North Temperate Zone with the mean maxima for the hottest month from 15° to 20° C. If this is the case, we are dealing with a species which extends in both directions from its normal zone. The more northern extensions may be explained by the fact that the very shallow and protected lagoons and interiors of prolonged and narrow bays preferred by this species may have the temperature of their waters raised through the action of the air and of the sun. In such waters, insolation undoubtedly is the most effective agent in raising the temperature as much as 10°–12° C. or even higher. To the south, the invasions of *Zostera marina* may be assumed to be made possible by the seasonal lowering of the temperature of the waters through the lower winter temperatures, *e.g.*, the winter temperatures on the coast of North Carolina is somewhat under 20° C. and the winter temperature on the coast of West Florida is also somewhat under 20° C. It would be expected, if the seasonal lowering of the waters south of the lower limits of the North Temperate Zone allows the eel-grass to find its normal temperature for fruiting in an earlier

season of the year than late summer, that the farther south the species grows, the earlier will be the fruiting season. Unfortunately, it is impossible to obtain any extensive data on this subject, but reliable testimony indicates that it flowers and fruits somewhat over a month earlier on the coast of New Jersey than it does on the coast of northern New England. It seems therefore that the critical temperature for persistence of this species, at least through flowering and seeding, is the same throughout its limits and that the species does not differ from a typical stenothermal species from this point of view. *Zostera marina,* however, is one of the most typical of the eurythermal species in that it must endure extremes of both heat and cold in various portions of its extensive range and in the various seasons of the year in each and every portion of its habitat. It is not known as to the temperature limits of the vital activity of the vegetative portions of the *Zostera,* but it does not seem possible that their separation can possibly be as wide as the differences between the extreme limits of the temperatures of endurance and probably are very much less. The *Zostera* probably has rather narrow limits to the temperature range of its vegetative activities and undoubtedly passes into a resting or hibernating condition, a condition of cold-rigor or of heat-rigor as the case may be, at the upper as well as at the lower portions of its temperature range. The land perennials of temperate zones do this and it seems safe to assume that *Zostera* does the same.

The case of *Ascophyllum nodosum,* a perennial brown alga of complex structure, is a very excellent one for study. This species ranges from the western coast of Greenland to that of New Jersey and it has a similar range on the northern and western European coast. On the coast of Greenland, it fruits in summer and it fruits earlier and earlier in the season as it proceeds towards the south, until, in the region of Long Island Sound, it fruits in late winter and early spring. The frond, or

vegetative portion, of *Ascophyllum* does not seem at all vigorous during the summer of the southern portion of its range. It seems perfectly evident that *Ascophyllum* is normal to the Upper Boreal Zone and invades the zones to the south because it finds, even on the northeastern coast of New Jersey, seasonal temperatures of proper duration below 10° C. The isocryme, or winter isotherm, of 5° C. touches the coast of New Jersey at about the point that marks the southern limit of the range of *Ascophyllum nodosum.* We have in this species, then, a eurythermal species whose critical temperature and amplitude for persistence range from 0° to 10° C. and which undoubtedly passes into a condition of heat rigor during the hotter months of the year in the southern portion of its range. It differs from the last example, in that its course of invasion is in one direction, viz., to the south.

Rhodochorton Rothii is a very delicate, filamentous, perennial red alga of very lowly stature. It has a range very similar to that of the last species and, in the southern portions of its range, fruits only in winter. The same things may be said of this species as were said of *Ascophyllum*. *Rhodochorton,* however, is a shade or cave plant in the more southern portions of its range, seeking the cooler portions of the warmer districts. This is doubtless its only opportunity of surviving the heat and is of great benefit to its delicate structure.

Monostroma Grevillei and *Polysiphonia urceolata* are annuals, with about the same range as the last two. They are summer annuals in the waters of Greenland, but are winter and early spring annuals of the southern portions of their range. With the exception, then, of the temperatures endured by their resting spores, they are confined to the temperature range of the Upper Boreal Zone and are practically stenothermal.

The last example quoted is *Grinnelia americana,* an annual red alga, apparently normal to the Long Island Sound district and therefore of the North Subtropical

Zone (20°–25° C.). North of Cape Cod, it is to be found only in certain warm protected spots where the insolation is sufficient to raise the temperature to that of the subtropical zones while the waters outside are those of the temperate zones. To the south of the North Subtropical Zone the species is a winter annual and follows the 20° C. isocryme. *Grinnelia* is, therefore, a stenothermal and not a typical eurythermal species and invades both colder and warmer zones, the colder because of warm spots and the warmer because of favorable seasonal conditions.

Farlow, in his Marine Algæ of New England, has amply explained still a different type of invasion, viz., from a colder zone into a warmer and I have some additional details in a paper soon to be published. The *Laminariaceæ*, or kelps, a number of species of perennial red algæ, some other browns, greens, reds, etc., pass Cape Cod and are to be found in the colder waters which are usually the deeper waters to the south of it. This seems to be an invasion from the North Temperate into the North Subtropical. It does not mean, however, as is the case also with the examples I have mentioned and discussed, that these seeming invaders are living in waters of a different range of temperature from that of the normal zone. Their eurythermy is but seeming, at least so far as this particular invasion is concerned.

In conclusion, I may say simply this: stenothermy is the rule both from the point of view of distribution and of physiology, at least so far as effective reproduction is concerned; eurythermy is largely, if not entirely, a matter of endurance of a wide range of temperature, much of which endurance is due to the power to enter into a condition of rigor after certain extremes of temperature of either direction are passed; and a study of the various reasons for zone invasion assists greatly in making these facts apparent.